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Genetic (Co)variances Among Birth Weight, 200-Day Weight, and Postweaning Gain in Composites and Parental Breeds of Beef Cattle¹

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ABSTRACT: Genetic and environmental (co)variances for birth weight, adjusted 200-d weight, and postweaning gain were estimated in nine parental and three composite populations of beef cattle. The parental breeds were Angus (A), Braunvieh (B), Charolais (C), Gelbvieh (G), Hereford (H), Limousin (L), Pinzgauer (P), Red Poll (R), and Simmental (S). The composites were MARC I ($\frac{1}{4}$ B, $\frac{1}{4}$ C, $\frac{1}{4}$ L, $\frac{1}{8}$ H, $\frac{1}{8}$ A), MARC II ($\frac{1}{4}$ G, $\frac{1}{4}$ S, $\frac{1}{4}$ H, $\frac{1}{4}$ A), and MARC III ($\frac{1}{4}$ R, $\frac{1}{4}$ P, $\frac{1}{4}$ H, $\frac{1}{4}$ A). Heritabilities of additive direct genetic effects for birth weight (.50) and postweaning gain (.49) were greater than for 200-d weight (.32). Heritabilities of additive maternal effects of .09 for birth weight and .10 for 200-d weight were much smaller than direct effect heritabilities. Heritabilities were larger in composites than in parental breeds for additive direct effects of all three traits but smaller for maternal 200-d weight. Correlations were high and positive for direct genetic effects of the three weight traits and higher in composites than in the parental breeds. Correlations between direct and maternal genetic effects for both

birth weight and 200-d weight were near zero. Some differences in variances among populations were correlated with differences in weight and milk yield. Heavier populations had larger variances, supporting the use of logarithmic transformation of weights to stabilize variances among genetic groups. Increased average milk yield was correlated with decreased phenotypic variance of 200-d weight. Average milk yield was also implicated in the expression of direct and maternal genetic effects for 200-d weight and their covariance. Comparison of univariate and multivariate estimates of genetic variances suggested that it is important to include birth weight in multivariate analyses of all weight traits to account for increased preweaning mortality of calves with extremely heavy or light birth weights. Based on heritability estimates, within-herd selection in composites should be at least as effective as in purebreds. Some differences among populations in genetic parameters were indicated, especially maternal 200-d weight and its correlations with other traits.

Key Words: Cattle, Growth, Breeds, Genetic Parameters, Milk Yield

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Introduction

Genetic (co)variance can differ among cattle populations for several reasons. Genetic variance in composite populations may be more or less than in the parental breeds (Mohd-Yusuff and Dickerson, 1991). Functional relationships, such as increasing variance with increasing average live weight, may also change genetic variance. Furthermore, estimates of genetic

variances may differ even when the variances themselves do not differ. Field data can be selectively reported and have poor data structure for estimation. Experimental and field data are both subject to loss of data due to death of animals. Techniques are now available to account for selection in the estimation of (co)variance. However, these techniques require the choice of an appropriate genetic model to be valid.

The objective of this study was to estimate the effects of growth rate, milk yield, and mating system on genetic (co)variances for birth weight, 200-d weight, and 168-d postweaning gain. The direct-maternal genetic covariance for 200-d weight was of particular interest because of differences among literature estimates. Multiple-trait, animal model REML procedures were used on experimental data to reduce bias in estimates of (co)variances, but simpler genetic models were also fitted to identify potential sources of bias in literature estimates.

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Materials and Methods

Animals. Gregory et al. (1991a) evaluated heterosis retention by comparing initial and advanced generations of composite populations to their parental populations. The three composites and proportions of the nine parental breeds in each composite were MARC I ($\frac{1}{4}$ Braunvieh, $\frac{1}{4}$ Charolais, $\frac{1}{4}$ Limousin, $\frac{1}{8}$ Angus, and $\frac{1}{8}$ Hereford), MARC II ($\frac{1}{4}$ Gelbvieh, $\frac{1}{4}$ Simmental, $\frac{1}{4}$ Angus, and $\frac{1}{4}$ Hereford), and MARC III ($\frac{1}{4}$ Pinzgauer, $\frac{1}{4}$ Red Poll, $\frac{1}{4}$ Angus, and $\frac{1}{4}$ Hereford).

Details of the formation of purebred and composite populations are given in Gregory et al. (1991a). The Angus and Hereford populations had been maintained at USMARC as closed breeding populations. The Gelbvieh, Limousin, Pinzgauer, and Simmental populations were established through a grade-up program from Angus and Hereford dams. Some purchased $\frac{3}{4}$ Gelbvieh dams graded-up from Charolais \times Angus dams were also added.

Purebred Brown Swiss females were purchased and bred to nine Braunvieh sires to establish a $\frac{3}{4}$ to $\frac{7}{8}$ Braunvieh population. The Charolais and Red Poll populations were established by purchasing purebreds. Additional Charolais females were obtained by grading up from Hereford-Angus crossbred females.

Selection and Mating. All yearling heifers were retained for breeding. From 1978 through 1984, nonpregnant females were retained unless they were nonpregnant in two successive years. Since 1985, all nonpregnant animals were removed from the experiment. Traits such as age, color, and extremes in skeletal size were used to remove excess females. Bulls that were extreme for weight, condition, muscle score, and skeletal anatomy were not selected for mating. Other factors used to identify bulls for use were reduced risk of dystocia and larger scrotal circumference (especially Hereford and Limousin). Polledness and color patterns of red or red with white markings were favored in identifying males for use in the composite populations. A broad pedigree base was maintained in each population, except carriers of genetic defects and their close relatives were avoided after they were identified.

Use of AI allowed most sires (> 80%) to be used in two or more years. Females were assigned to sires on an age-stratified random basis, except half-sib or closer matings were avoided.

Data. The three traits studied were birth weight, weaning weight adjusted to 200 d, and adjusted 168-d postweaning gain. Data used in the analyses started with birth weight in 1978 for most populations and ended with weaning weight in 1992. Pinzgauer data began in 1982 and MARC III in 1980.

Calves were weaned at an average age of 180 d but actual age varied with individual birth date and year. Weaning weight was adjusted to 200 d by linear

extrapolation on birth weight and actual weaning age and weight. Bulls and heifers were always weighed close to 168 d postweaning. Postweaning gain was adjusted to 168 d by multiplying 168 times postweaning ADG.

Until 1988, all males were left intact and fed a diet of corn silage, rolled corn, and supplement (2.69 Mcal of ME/kg) for 140 d following a 28-d adjustment period. Most male calves from the purebred populations and the F_3 generation of the composite populations born in 1988 through 1991 were castrated at an average age of 203 d and assigned to one of two finishing diets consisting of either 2.82 Mcal of ME/kg or 3.07 Mcal of ME/kg. They were serially slaughtered at an average age of 438 d, ranging from 204 to 267 d after castration. An intermediate weight closest to 168-d postweaning was used to calculate postweaning gain. Seven to nine males in each purebred and F_3 population and all F_4 males were left intact during this phase of the experiment.

Weights from twin animals were set to missing values. Weights that were more than 3 SD from the mean were checked for reasonableness based on subsequent weights and gestation length. Weights were set to missing if fewer than 10 calves of a given generation (F_1 , F_2 , or $F_3 + F_4$) of a composite were born in a year. Adjusted 200-d weights and 168-d postweaning gains of calves that were raised by foster dams were set to missing.

Pedigree information was obtained on all cattle back to as early as 1962. Calves from grade-up programs other than Braunvieh had to be at least $\frac{7}{8}$ blood. Pedigree information on twins and other animals was retained even if weight records were missing.

Analysis of Data. A derivative-free, multiple-trait REML program (Boldman et al., 1993) was used to estimate (co)variance components for each population. Fixed effects for birth weight and adjusted 200-d weight consisted of a group effect and dam's age. The group effect was defined by sex (male or female) and year. Group was further defined by generation (F_1 , F_2 , or $F_3 + F_4$) for the composite populations. Dam age was statistically modeled as linear and quadratic regression coefficients. Dam ages ranged from 2 to 5 because all cows older than 5 yr were set to a value of 5. A single fixed effect for postweaning gain consisted of a group defined by sex (bull, steer, or heifer), year, generation (composites only), and finishing diet (steers only).

Random effects fitted for birth weight and adjusted 200-d weight were additive direct genetic, additive maternal genetic, maternal common environment, and residual effects. Only additive direct genetic and residual effects were assumed for 168-d postweaning gain. All possible covariances among additive direct and maternal genetic effects were estimated. The covariance between maternal common environment effects for birth and 200-d weight was also estimated.

Table 1. Weight, milk, and numbers of weight records, sires, and maternal grandsires for each population

Population	No. of observations			Sires	Maternal grandsires	Weight, % ^a	Milk, % ^b
	Birth wt	200-d wt	168-d gain				
Angus	2,122	1,911	1,745	81	75	-11.67	-18.87
Braunvieh	1,464	1,321	1,163	62	53	5.62	23.38
Charolais	1,480	1,336	1,185	59	52	5.38	-8.51
Gelbvieh	1,303	1,174	1,124	55	45	4.58	11.22
Hereford	1,541	1,395	1,248	69	48	-12.02	-39.74
Limousin	1,563	1,409	1,244	60	51	-5.56	-10.64
Pinzgauer	883	794	697	42	31	6.24	12.37
Red Poll	1,407	1,300	1,143	54	47	-8.07	3.70
Simmental	1,494	1,302	1,165	70	61	5.21	14.76
MARC I	3,086	2,806	2,468	120	88	5.47	9.35
MARC II	3,733	3,465	3,128	117	93	4.19	2.79
MARC III	2,699	2,478	2,478	91	67	.63	.20
Total	22,775	20,691	18,459	880	711	—	—

^aWeight was determined as the average percentage deviation of unadjusted birth weight, 200-d weight, and 168-d postweaning gain.

^bMilk was determined from percentage differences in estimated 200-d milk yield based on three weigh/nurse/weigh observations on approximately 50 females per population (Gregory et al., 1992).

Each population was independently analyzed. The criterion for stopping the derivative-free iterative search procedure was when the variance of two times the log-likelihood in the Simplex was less than 1×10^{-10} . Analyses were restarted several times before and after reaching the stopping criterion to reduce the chance that the log-likelihood was at a local maximum.

Estimates of variance components for 368-d weight were constructed from the linear combination of (co)variance components for 200-d weight and 168-d gain (Lin and Allaire, 1977). Estimates of covariance components were also calculated as covariances with the linear combination (Bennett et al., 1991).

Reduced Genetic Models. A series of reduced genetic models was fitted to each of the populations to identify potential sources of bias in parameter estimates. The first reduced model eliminated covariances between different traits. The second reduced model eliminated covariances between traits and between direct and maternal genetic effects. The third reduced model contained only direct effects and no covariances between traits. Paired *t*-tests were used to test average changes in parameters between different models.

Analysis of (Co)variances. Variance and covariance components can differ due to changes in gene frequencies. These components can also differ due to functional relationships such as scaling of components with animal weight or restriction of growth by limited maternal nourishment. Multiple regression was used to isolate the effects of changes in gene frequencies brought about by purebred or composite mating systems from those due to differences in average weight or average amount of milk produced. Twelve estimates for each (co)variance component, one per

population, were regressed on mating system, weight, and milk (Table 1).

A single estimate of weight for each population was used as a covariate for all components estimated from that population. For each population, weight covariate was calculated as the average of deviations (percentage of the overall mean) for birth weight, 200-d weight, and 168-d postweaning gain. The covariate for milk was the deviation (percentage of the overall mean) for 200-d milk production estimated from three weigh/nurse/weigh observations on approximately 50 females per population over 2 yr (Gregory et al., 1992). The mating system covariate was coded as +1 for composite and -1 for purebred mating system.

Components from each population were weighted by the total number of observations of birth weight, 200-d weight, and 168-d postweaning gain in that population. Eight df were available to estimate the empirical residual variance and standard errors of the intercept and three regression coefficients. Covariates were dropped until the model with the lowest residual SD (**RSD**) was found. Real differences in populations with identical explanatory variables inflate the standard errors of the regression coefficients.

Genetic Parameters. Direct, total, and offspring-dam heritabilities were each calculated as proportions of phenotypic variance. Phenotypic variance was the sum of direct genetic, maternal genetic, direct-maternal genetic, maternal common environment, and residual (co)variance components. Direct heritability was estimated from direct genetic variance only. Total heritability was estimated from the sum of direct genetic variance, $.5 \times$ maternal genetic variance, and $1.5 \times$ direct-maternal genetic covariance (Willham, 1972). Offspring-dam heritability was estimated as the sum of direct genetic variance, maternal genetic variance,

and $2.5 \times$ direct-maternal genetic covariance. Correlations were calculated as genetic, common maternal environment, and residual covariances divided by the product of genetic, common maternal environment, and residual standard deviations of the two traits, respectively.

Results

Numbers of valid birth, 200-d, and postweaning gain records and the number of sires and maternal grandsires are given in Table 1 for each population. Weaning weight numbers were fewer than birth weight numbers because of death loss and eliminating foster records. Most of the additional decrease in postweaning gain numbers resulted from not including postweaning records from animals born in 1992. Also shown are weight and milk covariates for each population used in regression analyses.

Estimated variance components are shown in the Appendix tables. Six breeds (Braunvieh, Charolais, Hereford, Limousin, Pinzgauer, and Simmental) had one Eigenvalue approaching zero (not shown), indicating that their estimated genetic correlations were nearly out of the parameter space.

Direct, offspring-dam, and total heritabilities are shown in Table 2. Heritability estimates based on predicted offspring-dam regressions are included for comparison with literature estimates. Both offspring-dam and total heritabilities include estimated variances for direct and maternal effects and their covariance. Sampling variances between the direct-maternal genetic covariance and each of the variances

(Meyer, 1992) are negatively correlated. Meyer (1994) found that total heritability was less variable across different genetic models and suggested that it was estimated more accurately than an individual component.

Heritabilities for birth weight, 168-d gain, and 368-d weight were similar and .15 to .18 greater than for 200-d weight. Offspring-dam heritabilities averaged .10 to .15 greater than direct heritabilities. Total heritabilities were intermediate to the other two types of heritability estimates.

Intercepts and regression coefficients for mating system, weight, and milk are shown in Tables 3 to 7. Three equations for each (co)variance component are shown. The mean equation is the best single estimate of the component and its associated RSD can be compared with other equations. The full equation includes the intercept and all three covariates and adjusts each coefficient for the effects of all others. The lowest RSD equation is an attempt at developing a more parsimonious equation by sequentially deleting coefficients that did not exceed their SE. In some cases the mean equation or full equation was also the lowest RSD equation.

At least one of the explanatory variables was significant ($P < .05$) for 8 out of 10 genetic, common maternal environment, and residual variance components. Mean values of all covariances were positive and significant ($P < .05$) except for the covariances of direct genetic birth weight with either maternal genetic birth weight or 200-d weight, the genetic covariance between direct and maternal 200-d weight, and the covariance of common maternal environments for birth weight and 200-d weight.

Table 2. Heritability estimates for birth weight, 200-d weight, 168-d gain, and 368-d weight

Population	Direct				Offspring-dam ^a		Total ^b	
	Birth wt	200-d wt	168-d gain	368-d wt	Birth wt	200-d wt	Birth wt	200-d wt
Angus	.26	.25	.45	.42	.42	.34	.34	.28
Braunvieh	.44	.32	.48	.51	.68	.61	.58	.48
Charolais	.43	.16	.46	.34	.70	.21	.59	.18
Gelbvieh	.38	.33	.45	.47	.74	.44	.59	.38
Hereford	.54	.23	.39	.27	.42	.19	.46	.19
Limousin	.47	.26	.45	.40	.45	.35	.45	.30
Pinzgauer	.62	.49	.51	.62	.89	.56	.77	.53
Red Poll	.66	.34	.45	.54	.43	.55	.50	.46
Simmental	.46	.24	.50	.41	.40	.46	.41	.35
MARC I	.56	.40	.49	.55	.72	.54	.65	.48
MARC II	.54	.36	.50	.54	.71	.42	.64	.39
MARC III	.54	.34	.59	.55	.67	.48	.61	.42
Purebred avg	.47	.29	.46	.44	.57	.41	.52	.35
Composite avg	.55	.37	.53	.55	.70	.48	.63	.43

^aSum of direct genetic variance, $.5 \times$ direct-maternal genetic covariance, and $1.5 \times$ direct-maternal genetic covariance divided by phenotypic variance.

^bSum of direct genetic variance, direct-maternal genetic covariance, and $2.5 \times$ direct-maternal genetic covariance divided by phenotypic variance.

Table 3. Regressions of direct genetic (co)variances on mating system, weight, and milk yield

Equation	Intercept	Regression coefficients			RSD
		Mating ^a	Weight ^b	Milk ^c	
Variance (birth wt), kg ²					
Mean ^d	15.08 ± 1.67**				5.76
Full ^e	15.25 ± 1.23**	2.04 ± 1.38	.43 ± .33	.02 ± .14	4.18
Lowest RSD ^f	15.25 ± 1.15**	2.00 ± 1.28	.47 ± .19*		3.93
Variance (200-d wt), kg ²					
Mean	179.02 ± 15.39**				53.33
Full	183.53 ± 10.97**	27.86 ± 12.18 [†]	.58 ± 2.94	1.36 ± 1.19	37.03
Lowest RSD	183.88 ± 10.25**	28.80 ± 10.55*		1.56 ± .70 [†]	35.02
Variance (168-d gain), kg ²					
Mean	216.90 ± 12.76**				44.21
Full	217.70 ± 6.81**	13.70 ± 7.57	4.90 ± 1.83*	-.21 ± .74	23.00
Lowest RSD	217.91 ± 6.42**	14.07 ± 7.06 [†]	4.51 ± 1.05**		21.79
Covariance (birth wt × 200-d wt), kg ²					
Mean	30.90 ± 5.21**				18.06
Full	32.10 ± 4.40**	8.27 ± 4.88	.58 ± 1.17	.23 ± .47	14.83
Lowest RSD	31.89 ± 4.18**	7.88 ± 4.59	1.01 ± .68		14.18
Covariance (birth wt × 168-d gain), kg ²					
Mean	24.42 ± 4.88**				16.89
Full	25.39 ± 3.29**	7.96 ± 3.66 [†]	1.11 ± .88	.06 ± .37	11.11
Lowest RSD	25.35 ± 3.09**	7.86 ± 3.39*	1.21 ± .51*		10.49
Covariance (200-d wt × 168-d gain), kg ²					
Mean	128.16 ± 15.62**				55.12
Full	134.91 ± 7.26**	36.64 ± 8.07**	-1.83 ± 1.95	2.35 ± .80*	24.52
Lowest RSD	133.82 ± 7.12**	33.62 ± 7.35**		1.75 ± .47**	24.36

^aCovariate values of +1 for composites and -1 for purebreds.

^bWeight covariate (%) is shown in Table 1.

^cMilk yield covariate (%) is shown in Table 1.

^dIntercept only.

^eAll covariates included.

^fOnly covariates resulting in the lowest RSD included.

[†] $P < .10$.

* $P < .05$.

** $P < .01$.

Discussion

Effects of Weight. Increased weight was associated with increased direct genetic variances for birth weight and 168-d gain and their covariance (Table 3), and decreased covariance between genetic direct and maternal 200-d weight (Table 5). Increased weight was also associated with increased common maternal environment for 200-d weight (Table 6), and increased residual variances for birth weight, 200-d weight and 168-d gain and covariance of 200-d weight and 168-d gain (Table 7). A probable explanation for these increases is the scaling of variation to body weight. If standard deviation is scaled proportionally to weight, then a 1% increase in weight should increase variance by 2%. Regression coefficients of phenotypic variance on mating system, weight, and milk are shown in Table 8. Regressions on weight show 3.3% (± 1.0), 2.3% ($\pm .4$), 2.5% ($\pm .5$), and 1.9% ($\pm .3$) increases in phenotypic variances of birth weight, 200-d weight, 168-d gain, and 368-d weight, respectively, per 1% increase in weight. Individual genetic and residual components of variance were

variable but did not significantly differ from 2% increase in variance component per 1% increase in weight.

These results suggest that using the logarithm of weight would standardize variances among genotypes of different weights. However, Garrick et al. (1989) found that logarithms of birth weight, weaning weight, and postweaning gain did not equalize variances of different sexes or percentage of Simmental ancestry.

Effects of Milk. Increased milk level tended to increase the direct genetic variance of 200-d weight and its covariance with 168-d gain and maternal genetic 200-d weight (Tables 3 and 5). A nonsignificant reduction in maternal genetic 200-d variance (Table 4) was large and potentially important given the 63% range in average 200-d milk yield. Residual and common maternal variances of 200-d weight also decreased, as did the residual variance of 168-d gain and its covariance with 200-d weight (Tables 6 and 7). Increased milk significantly ($P < .05$) reduced phenotypic variance of 200-d weight (Table 8).

Table 4. Regressions of maternal genetic (co)variances on mating system, weight, and milk yield

Equation	Intercept	Regression coefficients			RSD
		Mating ^a	Weight ^b	Milk ^c	
Variance (birth wt), kg ²					
Mean ^d	2.59 ± .33**				1.17
Full ^e	2.63 ± .35**	.12 ± .39	-.04 ± .10	.04 ± .04	1.19
Lowest RSD ^f	2.59 ± .31**			.04 ± .02	1.09
Variance (200-d wt), kg ²					
Mean	56.74 ± 8.50**				29.40
Full ^g	52.40 ± 6.93**	-21.50 ± 7.72*	2.70 ± 1.85	-1.13 ± .76	23.43
Covariance (birth wt × 200-d wt), kg ²					
Mean	3.44 ± 1.28*				4.38
Full	2.96 ± 1.28*	-2.59 ± 1.42	.27 ± .35	-.04 ± .14	4.32
Lowest RSD	3.13 ± 1.19*	-1.77 ± 1.19			4.07

^aCovariate values of +1 for composites and -1 for purebreds.

^bWeight covariate (%) is shown in Table 1.

^cMilk yield covariate (%) is shown in Table 1.

^dIntercept only.

^eAll covariates included.

^fOnly covariates resulting in the lowest RSD included.

^gLowest RSD also.

* $P < .05$.

** $P < .01$.

These results are consistent with milk yield potentially limiting the expression of differences in preweaning growth. As milk yield increases, milk becomes less limiting on calf growth, resulting in increased direct genetic variance and decreased maternal genetic variance for 200-d weight. Because 200-d weight direct genetic effects are less likely to be suppressed if milk yield is high, the covariance with postweaning growth increases also. Residual and common maternal effects would also be reduced when milk yield is high because milk yield would not add to their variance if it exceeds the maximum required. This would also reduce residual variance of postweaning gain because 200-d weight is a component of difference in start and final weights used to calculate 168-d gain.

Koch and Clark (1955) reasoned that selection for weaning weight in an environment in which the influence of milk was removed would result in more emphasis on direct genetic effects, but they did not suggest an actual increase in genetic variance. MacNeil et al. (1992) suggested that the severe nutritional environment in which Line 1 Herefords were developed may have limited the expression of maternal effects which in turn limited the expression of direct effects for preweaning growth. Parallels can be drawn between the interaction of direct and maternal effects on weaning weight and the model of ovulation rate and uterine capacity effects on litter size in pigs (Bennett and Leymaster, 1989). More of the direct effect differences are realized as weaning weight differences of calves nursing high-milking cows, just as more of the ovulation rate differences are realized as litter size differences in high-uterine-capacity sows.

Effects of Mating System. After adjusting for weight and milk using covariates, direct genetic variances were larger in composites than in purebreds by 30% for birth weight, 36% ($P < .10$) for 200-d weight, and 13% for 168-d gain (Table 3). Covariances among direct traits increased proportionately more (49 to 62%) than variances resulting in higher genetic correlations among direct effects. These increases suggest that genes contributing to increased direct genetic variance in growth of composites had general effects on growth extending from conception to yearling age rather than independent effects at different stages of growth. Conversely, maternal genetic 200-d weight was reduced 82% in composites (Table 4). Residual variance for 168-d gain was reduced 13% in composites (Table 7).

Phenotypic variance for 368-d weight calculated as the sum of 200-d weight and 168-d gain was increased 11% ($P < .01$) in composites (Table 8) due almost entirely to the increased direct genetic covariance between 200-d weight and 168-d gain. Phenotypic variance was not significantly increased for either 200-d weight or 168-d gain in composites (Table 8). Because composites are heavier and have more milk than their contributing purebreds (Gregory et al., 1991b, 1992), actual variances would include the adjusted mating system difference plus the adjustments for weight and milk.

Increases in variance of direct genetic effects for weights and gain are consistent with an increase in heterozygosity and recovery from inbreeding depression in composites. Using the simplest assumption of variance within inbred lines being reduced proportional to the inbreeding coefficient and that an

Table 5. Regressions of direct genetic \times maternal genetic covariances on mating system, weight, and milk yield

Equation	Intercept	Regression coefficients			RSD
		Mating ^a	Weight ^b	Milk ^c	
Covariance (direct birth wt × maternal birth wt), kg ²					
Mean ^d	.62 ± .58				1.98
Full ^e	.49 ± .53	−.21 ± .60	.29 ± .14 [†]	−.06 ± .06	1.79
Lowest RSD ^f	.58 ± .49		.16 ± .08 [†]		1.71
Covariance (direct 200-d wt × maternal birth wt), kg ²					
Mean	9.59 ± 1.44**				4.98
Full	9.77 ± 1.28**	1.36 ± 1.42	.19 ± .35	.10 ± .14	4.30
Lowest RSD	9.88 ± 1.21**	1.67 ± 1.26		.14 ± .08	4.14
Covariance (maternal birth wt × direct 168-d gain), kg ²					
Mean	10.55 ± 1.40**				4.88
Full	10.23 ± 1.42**	−1.21 ± 1.58	.43 ± .39	−.02 ± .16	4.81
Lowest RSD	10.45 ± 1.30**		.35 ± .21		4.46
Covariance (direct birth wt × maternal 200-d wt), kg ²					
Mean	.88 ± 1.98				6.87
Full	1.23 ± 2.02	.99 ± 2.24	−.47 ± .53	.35 ± .23	6.79
Lowest RSD	.93 ± 1.83			.21 ± .12	6.34
Covariance (direct 200-d wt × maternal 200-d wt), kg ²					
Mean	2.96 ± 6.21				21.52
Full ^g	5.16 ± 2.88	7.55 ± 3.21*	−2.47 ± .78*	1.83 ± .31**	9.73
Covariance (direct 168-d gain × maternal 200-d wt), kg ²					
Mean	26.48 ± 7.28**				25.22
Full	25.64 ± 7.10**	−8.91 ± 7.88	−1.19 ± 1.89	1.13 ± .78	23.93
Lowest RSD	24.92 ± 6.77**	−10.90 ± 6.97		.74 ± .45	23.13

^aCovariate values of +1 for composites and -1 for purebreds.

^bWeight covariate (%) is shown in Table 1.

^cMilk yield covariate (%) is shown in Table 1.

^dIntercept only.

^eAll covariates included.

^fOnly covariates resulting in the lowest RSD included.

^gLowest RSD also.

[†] $P < .10$.

* $P < .05$.

** $P < .01$.

average of .76 of the reduction was recovered in the composites, the direct variances suggest that the inbreeding occurring in population formation and subsequently is in the range of 17 to 47% from their common base. The lack of increases in residual (co)variances for the three traits suggests no large increases in nonadditive variation within the composite populations. This is not consistent with the approximately 6% heterosis retained in the composites for these traits (Gregory et al., 1991a).

There is no apparent explanation for a reduction in maternal genetic variance for 200-d weight after adjusting for differences in average milk yield. It is possible that increased direct and decreased maternal genetic variance for 200-d weight are simply the result of negatively correlated estimation errors (Meyer, 1992) not accounted for by the regression analysis of each component separately. Differences in purebred and composite variance could arise from some unidentified systematic bias related to the somewhat different data structures of overlapping generations in purebreds and discrete generations in composites. A genetic explanation for reduced variance in composites

is dominance and overdominance (Mohd-Yusuff and Dickerson, 1991). Gregory et al. (1992) reported an average retained heterosis of 14.1% for estimated 200-d milk production consistent with high levels of dominance.

Heritabilities. Heritability estimates (Table 9) for direct genetic effects on birth weight, 168-d gain, and 368-d weight were similar and larger than those for 200-d weight. Heritability estimates for direct genetic effects on birth weight, 200-d weight, 168-d gain, and 368-d weight were higher than the weighted estimates given by Koots et al. (1994a). This is especially true in the composites, for which heritabilities were increased by .08 to .11 compared to purebreds. On the other hand, maternal genetic heritabilities for birth weight in purebreds and birth and 200-d weight in composites were lower than the weighted estimates (Koots et al., 1994a).

Meyer et al. (1993) compared heritabilities of experimental Hereford and multibreed synthetic Wokulups. Those differences closely parallel the differences in Table 9 between purebred and composites for direct and maternal heritabilities of birth weight,

Table 6. Regressions of maternal common environmental (co)variances on mating system, weight, and milk yield

Equation	Intercept	Regression coefficients			RSD
		Mating ^a	Weight ^b	Milk ^c	
Variance (birth wt), kg ²					
Mean ^{dg}	.76 ± .12**				.43
Full ^e	.72 ± .12**	-.14 ± .14	.06 ± .04	-.02 ± .02	.43
Variance (200-d wt), kg ²					
Mean	69.75 ± 9.86**				34.15
Full	67.92 ± 6.17**	-2.94 ± 6.81	3.15 ± 1.67 [†]	-2.74 ± .68**	20.86
Lowest RSD ^f	68.45 ± 5.76**		2.88 ± 1.44 [†]	-2.70 ± .64**	19.90
Covariance (birth wt × 200-d wt), kg ²					
Mean ^{dg}	1.79 ± .86 [†]				2.98
Full	1.93 ± .99 [†]	.82 ± 1.09	-.06 ± .27	-.02 ± .10	3.29

^aCovariate values of +1 for composites and -1 for purebreds.^bWeight covariate (%) is shown in Table 1.^cMilk yield covariate (%) is shown in Table 1.^dIntercept only.^eAll covariates included.^fOnly covariates resulting in the lowest RSD included.^gLowest RSD also.[†] $P < .10$.** $P < .01$.

Table 7. Regressions of residual (co)variances on mating system, weight, and milk yield

Equation	Intercept	Regression coefficients			RSD
		Mating ^a	Weight ^b	Milk ^c	
Variance (birth wt), kg ²					
Mean ^d	10.82 ± .51**				1.77
Full ^e	10.70 ± .39**	-.37 ± .43	.25 ± .10*	-.02 ± .04	1.32
Lowest RSD ^f	10.76 ± .35**		.19 ± .06*		1.23
Variance (200-d wt), kg ²					
Mean	255.31 ± 12.92**				44.79
Full	251.42 ± 9.59**	-6.85 ± 10.64	8.70 ± 2.57**	-2.32 ± 1.05 [†]	32.32
Lowest RSD	252.70 ± 9.05**		8.04 ± 2.28**	-2.20 ± 1.01 [†]	31.25
Variance (168-d gain), kg ²					
Mean	229.26 ± 9.32**				32.28
Full ^g	225.02 ± 6.15**	-14.42 ± 6.83 [†]	6.36 ± 1.65**	-1.28 ± .68 [†]	20.74
Covariance (birth wt × 200-d wt), kg ²					
Mean	14.59 ± 1.56**				5.39
Full	14.13 ± 1.56**	-1.52 ± 1.75	.70 ± .43	-.14 ± .16	5.31
Lowest RSD	14.51 ± 1.48**		.35 ± .23		5.10
Covariance (birth wt × 168-d gain), kg ²					
Mean	6.15 ± 1.32**				4.55
Full	6.28 ± 1.40**	.74 ± 1.54	-.12 ± .37	-.10 ± .14	4.69
Lowest RSD	6.13 ± 1.23**			-.12 ± .08	4.26
Covariance (200-d wt × 168-d gain), kg ²					
Mean	24.34 ± 6.40**				22.16
Full ^g	23.76 ± 2.59**	4.05 ± 2.88	3.21 ± .70**	-2.08 ± .29**	8.72

^aCovariate values of +1 for composites and -1 for purebreds.^bWeight covariate (%) is shown in Table 1.^cMilk yield covariate (%) is shown in Table 1.^dIntercept only.^eAll covariates included.^fOnly covariates resulting in the lowest RSD included.^gLowest RSD.[†] $P < .10$.* $P < .05$.** $P < .01$.

Table 8. Regressions of phenotypic variances on mating system, weight, and milk yield

Phenotypic variance	Regression coefficients				RSD
	Intercept	Mating ^a	Weight ^b	Milk ^c	
Birth wt, kg ²	29.79 ± 1.16**	1.43 ± 1.29	.97 ± .31*	-.03 ± .13	3.92
200-d wt, kg ²	560.42 ± 8.63**	4.12 ± 9.58	12.65 ± 2.31**	-3.00 ± .94*	29.13
168-d gain, kg ²	442.71 ± 8.03**	.72 ± 8.92	11.25 ± 2.15**	-1.48 ± .88	27.12
368-d wt ^d , kg ²	1346.08 ± 14.62**	75.90 ± 16.23**	25.04 ± 3.92**	-2.79 ± 1.60	49.35

^aCovariate values of +1 for composites and -1 for purebreds.

^bWeight covariate (%) is shown in Table 1.

^cMilk yield covariate (%) is shown in Table 1.

^dCalculated as linear combination of 200-d weight and 168-d gain (co)variance components.

* $P < .05$.

** $P < .01$.

200-d weight, and yearling weight. Meyer et al. (1994) estimated the heritability of milk yield to be greater in Herefords than in Wokalups and suggested that some Wokalup dams may have had the ability to produce more milk than their calves could consume.

Common Maternal Environment. Little of the variance in birth weight could be attributed to common maternal (uterine) environment (Table 9) after removing the genetic components of sibs born to the same dam. Common maternal environment did influence variation in 200-d weight and was larger than estimated maternal genetic variation in composites. Meyer et al. (1993) found common maternal environment to be smaller than maternal genetic variance for 200-d weight.

Correlations. Birth weight is a component of 200-d weight. A regression of 1 kg 200-d weight per kilogram of birth weight is expected if there is no additional effect of birth weight on preweaning growth. Correlations (Table 9) between birth and 200-d weights for genetic maternal effects, common maternal environmental effects, and residual effects do not differ significantly from a hypothesis of no relationship between pre- and postnatal growth for these effects. The correlation between direct genetic effects for birth and 200-d weights was about twice the expectation, indicating a positive relationship between pre- and postnatal direct genetic effects. Correlations in purebreds between direct genetic effects and between maternal genetic effects were positive and similar to those summarized by Koots et al. (1994b). Direct genetic correlations were larger and the maternal genetic correlation was smaller in composites compared to purebreds. Genetic correlations between birth weight and postnatal weights and gains were smaller than .7, suggesting that postnatal growth can be increased without increasing birth weight.

Genetic correlations were near zero for direct and maternal birth weight, direct birth and maternal 200-d weights, and direct and maternal 200-d weights. Postnatal growth was moderately correlated with maternal birth weight and postweaning growth was moderately correlated with maternal 200-d weight. Genetic correlations of the direct effects with maternal

genetic birth weight and 200-d weight averaged .45 and .16 larger, respectively, than those summarized by Koots et al. (1994b). Average genetic correlations between direct and maternal 200-d weights do not reflect the systematic effects due to weight and milk yield (Table 5). Meyer et al. (1993) also showed the direct-maternal correlations to be small and statistically unimportant in experimental herds and suggested that larger negative estimates were the result of management practices or environmentally induced negative offspring-dam covariances in field data. Estimates of the genetic correlation between direct and maternal 200-d weight more negative than -.05 were found in Hereford, Charolais, Limousin, and Angus. These breeds account for many of the estimates of this correlation in the literature. Estimates larger than .05 were found for Red Poll, Braunvieh, Pinzgauer, MARC I, and MARC III, populations that are not well represented in the literature.

Univariate Estimation. Variances and covariances were reestimated using identical data, fixed effects, and genetic models except that all covariances between effects for different traits were set to zero. The only remaining covariances were between direct and maternal genetic effects for birth weight and for 200-d weight. Results are shown in Table 10. There were no significant differences in variance components for birth weight between multivariate and univariate estimation. Multivariate estimates of direct genetic variances were significantly greater than univariate estimates for 200-d weight (29%) and 168-d gain (14%). Multivariate estimates of residual variances were smaller than univariate estimates by 6% for 200-d weight and 4% for 168-d gain. Multivariate estimates of phenotypic variances for 200-d weight and 168-d gain were approximately 4% greater. Heritabilities for 200-d weight and 168-d gain were decreased by .06 ($\pm .013$) and .04 ($\pm .011$), respectively, when estimated with a univariate model.

Estimates of components of variance for birth weight were unaffected by the estimation method. Birth weight was recorded on essentially every animal. Adjusted 200-d weights and postweaning gain were also available on all living animals. However, these weights were not available on those animals

Table 9. Predicted^a genetic, common environmental, and residual parameters for purebreds and composite populations

Direct genetic h^2 and r								
Direct genetic	Direct genetic effects ^b							
	Purebred				Composite			
	Birth wt	200-d wt	168-d gain	368-d wt	Birth wt	200-d wt	168-d gain	368-d wt
Birth wt	.47				.55			
200-d wt	.52	.28			.67	.37		
168-d gain	.32	.56	.46		.55	.75	.52	
368-d wt ^c	.47	.87	.90	.44	.65	.93	.94	.55
Maternal genetic h^2 and r								
Maternal genetic	Maternal genetic effects ^d							
	Purebred				Composite			
	Birth wt	200-d wt			Birth wt	200-d wt		
Birth wt		.09				.08		
200-d wt		.39		.13		.11		.06
Direct-maternal genetic r								
Maternal genetic	Direct genetic effects ^e							
	Purebred				Composite			
	Birth wt	200-d wt	168-d gain	368-d wt	Birth wt	200-d wt	168-d gain	368-d wt
Birth wt	.08	.41	.49	.52	.14	.49	.40	.47
200-d wt	.01	-.02	.29	.16	.08	.13	.18	.17
Common maternal environment								
Common maternal environment	Common maternal environment ^f							
	Purebred				Composite			
	Birth wt	200-d wt			Birth wt	200-d wt		
Birth wt		.03				.02		
200-d wt		.16		.13		.36		.11
Residual e^2 and r								
Residual effect	Residual effects ^g							
	Purebred				Composite			
	Birth wt	200-d wt	168-d gain	368-d wt	Birth wt	200-d wt	168-d gain	368-d wt
Birth wt	.40				.32			
200-d wt	.29	.46			.27	.44		
168-d gain	.12	.08	.54		.12	.12	.48	
368-d wt	.28	.75	.72	.42	.26	.77	.73	.37

^aPredicted from full equations presented in Tables 3 to 7 using mating system average differences in weight and milk as covariates for purebred and composite populations.

^bHeritabilities on diagonal, genetic correlations below diagonal.

^c368-d weight calculated from linear combination of 200-d weight and 168-d weight.

^dMaternal heritabilities on diagonal, maternal genetic correlations below diagonal.

^eCorrelations between maternal genetic and direct genetic effects.

^fCommon environmental variance divided by total on diagonal, correlation below diagonal.

^gResidual variance divided by total on diagonal, residual correlations below diagonal.

that died before weaning. It is known that deaths occur more frequently among calves with either very light or heavy birth weights (Morris et al., 1986; Gregory et al., 1991a). Because birth weight is correlated with subsequent weights, the absence of

these weights would reduce their estimated variances in univariate analyses. Univariate analysis assumes that missing weights are random, whereas multivariate analysis accounts for any correlations between birth weight and subsequent missing weights.

Table 10. Changes in (co)variances with univariate estimation

Variance or covariance	Multivariate estimate, kg ²	Univariate	Reduced univariate	Direct univariate
		Difference ^a , kg ²	Difference ^b , kg ²	Difference ^c , kg ²
Direct genetic				
Birth wt	15.08	.26 ± .28	−1.15 ± .82	−2.43 ± .31**
200-d wt	179.02	40.61 ± 8.48**	−11.52 ± 6.34†	−110.17 ± 10.75**
168-d gain	216.90	27.09 ± 6.15**		
Maternal genetic				
Birth wt	2.59	.16 ± .18	.12 ± .15	
200-d wt	56.74	6.26 ± 4.77	1.19 ± 2.68	
Direct × maternal				
Birth wt	.62	.11 ± .13		
200-d wt	2.96	−3.28 ± 2.59		
Common maternal				
Birth wt	.76	−.05 ± .09	−.15 ± .08†	
200-d wt	69.75	−2.71 ± 3.40	−1.95 ± .78*	
Residual effects				
Birth wt	10.82	−.14 ± .13	.55 ± .42	−.88 ± .21**
200-d wt	255.31	−15.91 ± 4.29**	5.68 ± 3.20	−32.42 ± 6.20**
168-d gain	229.26	−9.61 ± 3.67*		
Phenotype				
Birth wt	29.84	.34 ± .09**	−.12 ± .09	−.04 ± .13
200-d wt	563.77	24.96 ± 4.68**	−.36 ± .40	−18.90 ± 2.05**
168-d gain	446.17	17.48 ± 2.73**		

^aMultivariate estimate – univariate estimate. Standard errors based on weighted variance of the paired differences.

^bUnivariate model with direct-maternal covariances minus univariate model without covariances. Standard errors based on weighted variance of the paired differences.

^cUnivariate model with direct and maternal genetic effects but no covariances minus univariate model with direct genetic effects. Standard errors based on weighted variance of the paired differences.

†*P* < .10.

**P* < .05.

***P* < .01.

These results suggest that birth weight should be included in multivariate estimation of subsequent weights or any trait correlated with birth weight. Computer programs that analyze sets of traits with a common univariate model sometimes require that all animals have complete information for all traits. This would likely bias estimates of birth weight as well as correlated traits. Simulation of beef cattle traits to test estimation procedures for bias and accuracy needs to account for the increased mortality of calves with heavier and lighter birth weights.

Reduced Univariate Models. Reduced univariate models omitting the covariances between direct and maternal effects for birth weight and 200-d weight were used to reestimate variances. Differences in variance estimates between full and reduced univariate models are shown in Table 10. The only significant difference in variance estimates between the full and reduced univariate models was a small increase in maternal common environment for 200-d weight. Differences in $-2 \times \log$ -likelihood approximate a chi-square distribution with 2 df and ranged from .70 to 3.02 for 11 of the 12 populations and 8.50 in Red Poll (correlations between direct and maternal effects of $-.53$ for birth weight and $.62$ for 200-d weight). The

combined difference in $-2 \times$ likelihood was 28.10 with 24 df, indicating no significant contributions of the direct-maternal genetic covariances. This conclusion is the same as that reached by regression of the multivariate covariance estimates.

The univariate model was further reduced to only direct genetic and residual effects (Table 10). Dropping maternal genetic and common environmental variances from the model increased estimates of direct genetic and residual variances for birth and 200-d weight by about the same amount as the maternal variances so that estimates of phenotypic variances were changed only slightly. Estimates of direct genetic variance were increased more than residual variance.

Gregory et al. (1995a,b,c) estimated variance components in three subsets (steers, females, and bulls) of the same animals analyzed here. Variance estimates were obtained by Henderson's Method 3 applied to a sire model. Pooled phenotypic standard deviations were 0 to 8% smaller and genetic standard deviations were 6 to 19% smaller than the multiple-trait REML estimates. Average estimates of heritability were .09 to .12 lower for birth weight, 168-d gain, and 368-d weight but .03 larger for 200-d weight. Heritabilities for purebreds were similar

for the two estimation methods but different for composites. Heritabilities for purebreds tended to exceed those for composites in the Method 3 analyses, but this was reversed in the REML analyses. It is difficult to explain how the differences in analyses would affect the results. Somewhat different fixed effects were used in the analyses, sexes were pooled in one analysis and populations were pooled in the other, some animals were eliminated from the Method 3 analysis so that there were data for all traits, and relationships other than through the sire were ignored by Method 3. Some of these differences would tend to make REML estimates of variance components larger than those from Method 3, but it is not apparent why purebred and composite estimates would be affected differently.

Implications

Higher heritability estimates suggest that within-herd selection for weight should be at least as effective in composite as in purebred beef cattle populations. There seems to be adequate genetic variation in birth weight that is independent of postweaning growth so that postweaning growth can be increased without obligatory increases in birth weight. The direct-maternal genetic correlation for 200-d weight seems to be near zero, although this relationship may be more antagonistic in populations with heavier weight and lower average milk yield. Increased mortality of calves with heavy or light birth weights can bias analyses of postnatal weights and gains.

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Appendix

Table 1. Direct genetic (co)variances

Population	Direct genetic (co)variances, kg ²					
	Birth wt (1)	200-d wt (2)	168-d gain (3)	(1) × (2)	(1) × (3)	(2) × (3)
Angus	4.656	107.206	163.593	4.886	-1.368	82.455
Braunvieh	13.007	176.147	222.093	29.938	21.225	150.925
Charolais	13.122	106.860	243.165	14.423	28.325	68.252
Gelbvieh	12.086	210.355	201.857	28.558	36.536	118.100
Hereford	10.217	118.131	130.926	16.157	2.568	21.945
Limousin	9.927	140.095	179.149	14.805	2.167	71.756
Pinzgauer	29.424	288.960	236.643	79.111	44.371	185.344
Red Poll	13.921	157.334	151.799	27.276	21.924	126.879
Simmental	14.285	128.715	253.146	14.087	1.282	74.459
MARC I	20.856	233.756	226.310	37.040	37.847	170.969
MARC II	19.531	214.978	256.613	49.570	36.499	181.225
MARC III	15.890	208.351	261.193	41.779	38.808	169.862

Table 2. Maternal genetic (co)variances

Population	Maternal genetic (co)variances, kg ²		
	Birth wt (1)	200-d wt (2)	(1) × (2)
Angus	2.527	62.804	2.609
Braunvieh	1.183	94.020	3.284
Charolais	1.695	78.941	.302
Gelbvieh	3.002	67.818	9.892
Hereford	1.224	102.935	9.487
Limousin	1.403	73.579	.049
Pinzgauer	3.660	21.134	7.870
Red Poll	3.547	23.004	1.765
Simmental	4.487	103.157	13.579
MARC I	4.337	25.041	2.662
MARC II	1.891	50.103	2.076
MARC III	2.239	28.053	-1.897

Table 3. Direct-maternal genetic covariances

Population	Direct-maternal genetic covariances ^a , kg ²					
	(1) × (4)	(2) × (4)	(3) × (4)	(1) × (5)	(2) × (5)	(3) × (5)
Angus	.216	10.781	12.083	.946	-9.343	16.737
Braunvieh	2.428	14.124	14.219	6.576	27.907	61.749
Charolais	2.634	12.682	8.878	-5.784	-19.381	-15.466
Gelbvieh	3.492	3.234	10.816	3.064	-1.154	46.614
Hereford	-1.341	-.002	7.687	-11.555	-48.317	38.386
Limousin	-.753	.200	5.938	8.767	-9.464	15.299
Pinzgauer	3.619	9.252	13.476	-.381	8.915	29.757
Red Poll	-3.364	5.183	1.144	-4.177	28.564	26.218
Simmental	-2.549	13.376	21.352	2.695	5.207	89.370
MARC I	.556	14.592	13.260	8.541	23.023	24.613
MARC II	1.784	11.057	12.308	-6.600	-5.121	3.780
MARC III	.636	11.016	4.971	6.860	21.735	27.407

^a(1) direct genetic birth weight, (2) direct genetic 200-d weight, (3) direct genetic 168-d postweaning gain, (4) maternal genetic birth weight, and (5) maternal genetic 200-d weight.

Table 4. Maternal common environmental (co)variances

Population	Maternal common environmental (co)variances, kg ²		
	Birth wt (6)	200-d wt (7)	(6) × (7)
Angus	.854	72.523	2.664
Braunvieh	.743	27.554	4.212
Charolais	1.288	143.160	4.018
Gelbvieh	.584	17.892	-3.232
Hereford	.772	132.416	2.527
Limousin	.247	92.106	-.677
Pinzgauer	.994	59.107	-.652
Red Poll	.364	57.778	4.584
Simmental	1.529	39.598	-3.296
MARC I	.173	58.380	.282
MARC II	1.162	55.461	5.662
MARC III	.663	85.745	.288

Table 5. Residual (co)variances

Population	Residual (co)variances, kg ²					
	Birth wt (8)	200-d wt (9)	168-d gain (10)	(8) × (9)	(8) × (10)	(9) × (10)
Angus	9.999	205.001	203.156	15.546	12.125	26.549
Braunvieh	12.277	229.485	244.449	16.630	1.051	.158
Charolais	11.713	347.519	291.752	24.103	7.135	51.484
Gelbvieh	12.952	337.417	246.749	15.832	-3.837	14.390
Hereford	8.207	216.381	202.839	9.649	7.333	65.450
Limousin	10.193	239.803	219.202	10.684	6.923	28.938
Pinzgauer	9.919	214.669	230.014	3.080	1.967	-11.824
Red Poll	6.796	190.122	188.914	6.253	4.154	-20.237
Simmental	13.649	262.055	258.252	25.259	12.592	5.963
MARC I	11.026	245.031	240.291	16.400	1.455	20.667
MARC II	11.970	285.938	252.619	14.552	8.872	40.970
MARC III	10.040	262.489	179.719	12.316	7.779	25.175

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